

# On the age and origin of the species flock of haplochromine cichlid fishes of Lake Victoria

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Recent suggestions concerning the age and origin of the flock of haplochromine cichlid fishes in Lake Victoria (East Africa) are considered. These accept as proven the suggestion that Lake Victoria dried out completely in the Late Pleistocene, was dry for several thousand years, and refilled *ca.* 12 400 years ago. Apart from the fact that other geophysical evidence contradicts this claim, its biological implications, which do likewise, have never been considered by those who have accepted it. Like those of all previous authors who have seized on the presence of the haplochromine flock of perhaps more than 600 species as evidence of extremely rapid evolution since the lake allegedly refilled, the account completely overlooks the fact that any such desiccation must have eliminated not only the haplochromine cichlids but the entire biota of the lake. Nevertheless, its present fauna not only includes the haplochromines but many other endemic organisms that would not be expected, and whose presence and history demand an explanation if the lake did indeed dry out. No such explanation has been offered, nor does such seem possible. The recent interpretation of events is questioned and rejected.

**Keywords:** Lake Victoria; alleged desiccation; fate of biota; evolution of cichlid fishes

## 1. THE PROBLEM

The investigations of Nagl *et al.* (2000) into the origin and age of the haplochromine cichlid fishes of Lake Victoria encounter difficulties from the outset because they accept as proven a belief that is not only subject to geophysical uncertainty, but is firmly contradicted by biological evidence. They accept the claim of Johnson *et al.* (1996), already seized upon by several authors who have been unaware of the real implications of this alleged event, that Lake Victoria dried out completely in the Late Pleistocene, remained dry for several thousand years, and refilled only *ca.* 12 400 years ago. As pointed out in a paper not cited by Nagl *et al.* (2000) such desiccation is completely at odds with the biological evidence (Fryer 1997). It implies several unproven, and I believe improbable, consequences, most obviously that the enormous endemic cichlid flock of the lake evolved in this short period of time, though this has already been cited several times as an outstanding example of rapid evolution, e.g. by Johns & Avise (1998) and Galis & Metz (1998). The latter say (p. 1) that the geological data indicate that Lake Victoria 'must have been completely dry... perhaps as recently as 12 400 years ago' (emphasis added), though this is not proven, and that its cichlid flock 'must have evolved within this extremely short time span from a single ancestral species'. Unlike such authors, and unlike Johnson *et al.* (1996), Nagl *et al.* (2000), I believe correctly, find it 'inconceivable... that all the mutations responsible for the morphological adaptations differentiating the flock's individual species arose within a mere 12 400 years' (p. 1060). This recognizes the enormous adaptive radiation in morphology, ecology and behaviour that took place during the evolution of these fishes, of which they say there are more than 300 species. There may be more than twice this number. The magnitude of this radiation seems not to have been appreciated by those who accept the rapid evolution implicit in the postulated desiccation. Speciation may certainly occur rapidly, but

without necessarily involving many (or even any) morphological changes. Here we are dealing not simply with explosive speciation but with adaptive radiation involving high levels of morphological differentiation. Its end-points include highly specialized fishes with complex morphological adaptations, especially of the skull, jaws and pharyngeal apparatus, as well as of body form, for such tasks as crushing bivalve and gastropod molluscs, catching other fishes, scraping algae from rocks, and many others. Some habits, such as acting as cleaners of other fishes and paedophagy (eating the eggs and young brooded in the mouths of female cichlids), as well as simple predation on other cichlids, could not have arisen until differentiation of the flock had proceeded for some time. Had the time available for radiation been as short as implied by the alleged desiccation episode, evolution must have proceeded with unprecedented rapidity. To give perspective, Darwin's finches, a mere 14 species frequenting several islands, are believed to have evolved over a period of two to four million years.

Having rejected the possibility that the many mutations necessary to produce the morphological specializations that characterize its haplochromine fishes could have arisen in *ca.* 12 000 years, but having accepted that Lake Victoria was dry some 12 400 years ago, Nagl *et al.* (2000) appear to face two irreconcilable facts. They also face the equally daunting problem of explaining where in the drought-stricken area any fishes that later provided colonizers of the refilled lake sought refuge. Booton *et al.* (1999) have already suggested that some differentiation may have been preserved in refuges. Just where such refuges were to be found has to be explained.

Nagl *et al.* (2000) favour riverine refuges. As long appreciated by students of African cichlid evolution, and as they point out, riverine cichlids are mostly generalized forms and radiation is 'apparently conditional upon the colonisation of a large lake' (Nagl *et al.* 2000, p. 1060). The lake need not in fact be particularly large. They conclude that the Lake Victoria flock 'originated *in situ* from a non-

specialised riverine founding population' some 12 400 years ago and that the flock 'must therefore have arisen within this short period of time' (p.1060). So expressed, this appears to contradict their statement quoted above and to be exactly the same as the belief held by Johnson *et al.* (1996) and others who accept the recent desiccation of Lake Victoria. Consideration of how Nagl *et al.* (2000) believe it differs is best deferred until other matters have been considered, but, as will become clear, it should be noted that they make a distinction between the accumulation of mutations and their expression.

What has been completely overlooked by all those who accept the recent desiccation of Lake Victoria is that, if the endemic cichlids evolved in such a short period of time, all the other endemic organisms in the lake must have done likewise. Not only the haplochromine cichlids but seven other families of fishes, Clariidae, Mochokidae, Mastacembelidae, Characidae, Mormyridae, Cyprinodontidae and Cyprinidae, have produced endemic species, or even genera, in Lake Victoria. The tilapiine cichlids, a different lineage from the haplochromines and less prone to extensive or rapid speciation, have also produced two large endemic species. One of these, *Oreochromis esculentus*, is an open-water phytoplankton eater that shuns rivers. There are also endemic bivalve and gastropod molluscs and crustaceans in Lake Victoria as well as species of several groups, as different as oligochaetes and algae, that are known only from the lake and may also prove to be endemic, but localities elsewhere are insufficiently studied for such status to be claimed with confidence. In short, if the desiccation story is correct, attributes for which cichlid fishes are so renowned (but which I do not believe include the ability to produce several hundred, sometimes highly differentiated, species from a single ancestor—or even a few ancestors—in *ca.* 12 000 years) must be widely shared with other organisms. Such rapid evolution in several different groups would be unprecedented and is clearly unsupportable. On all generally accepted biological criteria some of the endemics have clearly adapted over a long period of time. A striking example at the generic level is the endemic clariid catfish *Xenoclarias* of which the two described species are in fact conspecific (Gee 1975). *Xenoclarias eupogon* chiefly frequents deep water for which it shows striking morphological specializations. Its suprabranchial chamber is greatly reduced and it lacks both the suprabranchial arborescent organs and gill fans that are so conspicuous in *Clarias*. Its presence indicates beyond reasonable doubt that Lake Victoria was not dry some 12 400 years ago. While *Clarias* has both aerial and aquatic respiratory areas, *Xenoclarias* is equipped solely for aquatic respiration. As Gee (1975, p.216) noted, its 'preferred deep water habit and the absence of accessory respiratory organs, along with the ability to breed in the lake [i.e. without entering inflowing streams to spawn as do some of Lake Victoria's non-cichlid fishes] all seem to indicate that *Xenoclarias* originated in a lacustrine environment'. Incidentally *X. eupogon* is most abundant at depths of 50–79 m and Gee (1975) made specific reference to individuals collected at 75 m whereas Johnson *et al.* (1996) give the maximum depth of Lake Victoria as 69 m, which contradicts information given by Johnson (1996) whose bathymetric map includes a 75 m contour line. In a

drought situation it would be difficult for a deep-water specialist such as *X. eupogon* to find a refuge outside the lake. Likewise, if they existed, streams would be unsuited to such an open-water lacustrine fish as *O. esculentus* and completely so to the endemic, planktonic, diaptomid copepod *Tropodiatomus stuhlmanni*, to cite but three examples.

## 2. GEOPHYSICAL CONTRADICTIONS

While the data relating to the desiccation of Lake Victoria presented by Johnson *et al.* (1996) appear convincing, though not conclusive, so does contrary evidence. Thus, as Johnson (1996) himself recorded, it appears that Lake Albert, which lies within less than 250 km of Lake Victoria, and is smaller and shallower, and must have had a reasonably similar climate, has never dried out in the last 30 000 years or so. Yet if Lake Victoria did so or even fell below the level of its outlet, Lake Albert would have been deprived of a major source of its water. A core taken in Lake Victoria itself at a depth of only 9 m by Kendall (1969) which Johnson (1996) accepted as the best dated sequence of climatic change for any of the large east African lakes, was radiocarbon dated at regular intervals along its length. This revealed an unbroken accumulation of sediment to almost 14 000 years before present (BP), by which time, according to Johnson *et al.* (1996), the lake had been dry for well over 1000 years. Furthermore, the core was taken inshore, a region that would be exposed before much deeper areas if the lake contracted. A map of suggested shorelines given by Stager *et al.* (1986) suggested that the lake shrunk to an area of *ca.* 15 000 km<sup>2</sup> *ca.* 13 000 years BP, which is far from complete desiccation (for amplification of such evidence see Fryer (1997)). The difficulty in obtaining precise physical data is indicated by the uncertainty surrounding such an apparently simple fact as the maximum depth (see §1) for which different figures are given by different authors.

Although more concerned with changes in hydrology, Beuning *et al.* (1997), of whom three contributors are co-authors of Johnson *et al.* (1996), subscribe to the desiccation theory and provide some relevant information. However, their account includes ambiguities and 'apparent contradictions' of previous studies that they admit were 'difficult to reconcile', which weakens rather than supports the case. Although Johnson *et al.* (1996) claimed that the lake began to fill at *ca.* 12 400 years BP, Beuning *et al.* (1997) suggest that, at *ca.* 13 000 years BP, Lake Victoria was a 'relatively shallow closed lake' and record sedimentation rates as early as 13 240 years BP, even though all age estimates were reduced by 500 years by applying a 'correction factor' in order to compensate for the anomaly that present-day surface sediments gave an age reading of 500 years.

These may be minor discrepancies, but two basal dates from 'grassy charcoal, presumably of terrestrial origin' could have been from material washed in at a time of low water level. Indeed, the younger date at least falls within the period when they say the area was occupied by a shallow lake. Other uncertainties include a 'paradoxical effect' where sediments that differ in age by more than 2300 years are separated by only a few centimetres of

material instead of the expected 1.5 m or more, 'although the sediment record appears uniform'. This is said to be 'best explained as a hiatus', which is a description of the situation, not an explanation, and says nothing about what happened to the missing sediments. They also report 'an apparent age reversal' where older sediments overlies younger deposits. This they attribute to 'reworking of older sediment components', which is difficult to understand. Such uncertainties undermine confidence and show how imprecise such observations can be.

No consideration is given to the biological implications of the alleged desiccation by either group of authors other than the here rejected alleged rapid evolution of cichlid fishes, but these implications cannot be ignored. When fossils of molluscs that inhabit warm climates were found in gravels supposedly deposited in a glacial period (Schaefer 1953), this refuted the inferences relating to climate that had been drawn from these gravels, which were in fact partly of interglacial age. The presence of endemic fishes of several families and of endemic invertebrates similarly negates the suggestion that Lake Victoria refilled little more than 12 000 years ago after a long period of desiccation.

### 3. HOW DID THE FAUNA COPE WITH THE ALLEGED DESICCATION?

If Lake Victoria did dry out and then remained dry for many years, the animals present would have been exterminated unless they managed to escape to refuges elsewhere (which is unlikely; see below). One therefore asks, whence came the fishes and other aquatic organisms that recolonized the later refilled basin? So far as its cichlid fishes are concerned, Nagl *et al.* (2000) attempt to answer this question using molecular evidence. All its haplochromines belong to just one of seven haplogroups recognized in a survey of a wide area of eastern Africa. Of this there are four subgroups. One subgroup (VD), which may be a single species or a species complex, is confined to Lake Victoria. All the other Lake Victoria endemics belong to a subgroup (VC) that, with one exception, is confined to the lake or its affluent streams. The exception is from Lake Singida in the Eyasi drainage, which is easily explained by river capture or the crossing of a swampy watershed and is in no way anomalous. The other subgroups comprise species from the Lake Edward-George and Lake Albert areas (VB) and the Lake Rukwa drainage (VA), respectively. (*Tissichromis laparogramma* belongs to subgroup VC, but one individual was unaccountably diagnosed as belonging to VB and a sequence of *Prognathochromis paraguarti* elucidated by Meyer *et al.* (1990) also has a VB haplotype.) The divergence times of these subgroups 'are clearly in excess of 12 400 years' and 'must have existed in distinct lineages well before the colonisation of the modern L. V[ictoria]' (Nagl *et al.* 2000, p.1058) (that is on the assumption that the lake dried out). These findings are particularly significant in that, apart from the Lake Singida locality, which is unimportant in this context, they give no indication of sites outside the Lake Victoria basin in which fishes from the lake could have found refuge during the supposed Late Pleistocene desiccation.

Nagl *et al.* (2000) suggest that subgroup VD 'may encompass descendants of the species that survived the desiccation of the Palaeolake either in rivers crossing the basin or in persisting pools' (p.1057). However, it is alleged that the desiccation lasted for several thousand years and, as already pointed out (Fryer 1997), in a period of prolonged aridity, if Lake Victoria (present area of more than 68 600 km<sup>2</sup>) dried out completely, so too and more readily would inflowing streams and adjacent pools and swamps. Indeed, of all places that might retain sufficient water to support fishes and other aquatic organisms during a period of widespread and persistent aridity in the area, much the most likely is Lake Victoria itself. As it diminished in size, fishes would follow the retreating water and remain within the basin. If Lake Victoria dried out there would be no permanent streams in the area. If, in spite of the aridity, permanent or even intermittent streams persisted, these would discharge into the closed basin of Lake Victoria where a remnant lake would perhaps remain. This situation, and the lack of evidence of colonization from the Nile, with which the molecular evidence of Nagl *et al.* (2000) is in accord, is discussed elsewhere (Fryer 1997). Moreover, we lack evidence of even any putative refuges that could have sheltered cichlid fishes and other organisms if Lake Victoria did indeed dry out. To suggest any such refuges is very difficult and to explain how they were reached even more so. Furthermore, if such an event occurred, the cichlids involved would be suited to a lacustrine lifestyle and ill-adapted to life in streams. I suggest that, if there had been a drought sufficiently severe to dry out Lake Victoria, its fishes would have suffered extinction, just as did those of a previous lake or lakes that occupied part of the present basin in Miocene times, when even a fish like *Polypterus*, which can use atmospheric air, perished (Greenwood 1951).

### 4. THE DATING OF EVENTS

Although Meyer *et al.* (1990) cite Temple (1969) as giving the age of Lake Victoria as between 250 000 and 750 000 years, that author in fact cautiously confined his suggested time of origin to the Mid-Pleistocene. On the basis of molecular evidence, Meyer *et al.* (1990) estimated that its cichlid flock may be less than 200 000 years old and that these fishes shared a common ancestor with *Astatoreochromis* ca. 3.5 million years (Myr) ago. Such estimates have to be treated with caution. L. S. Kaufman (personal communication) and his colleagues concluded that not enough is known about molecular clocks in these fishes to give sensible information over short time-periods. Earlier events in cichlid evolution deduced by modern methods (electrophoresis) (Sage *et al.* 1984) have been shown by fossil finds to have happened more than twice as long ago as so estimated (Van Couvering 1982).

Nagl *et al.* (2000) provide trees showing the sequences of origin of the various groups of East African haplochromines and attempt to date their divergence times. Dating the various nodes, such as those of the haplo-morphs revealed, is based on tenuous evidence and involves admitted uncertainties, partially to avoid which they calculate a range of such times. Node 2 involves an estimate of the age of Lake Malawi. As the estimates

range from 2 to 4 Myr, both values are used and two estimates of the times of ever more finely discriminated events, down to the separation of subgroups of haplo-morphs, are given in their table 2 based on these initial differences. The route to the terminal subgroups, which involves the use of estimates derived from work on sharks, is tortuous. Moreover, not only are alternative times with approximately twofold differences given for each node, but abstruse calculations using four approaches are used to provide eight estimates of the divergence times for each node, four of them being essentially double those of the other four. Notwithstanding the extreme crudeness of these estimates, a standard error, given to two, occasionally three places of decimals is indicated for each. Crude means would be just as informative as such pseudo-precision.

Although Nagl *et al.* (2000) agree that the Lake Victoria haplochromines had a riverine origin, they give little consideration to riverine forms. They say that, because of taxonomic difficulties, no attempt was made to identify such forms to species level, yet in an earlier paper (Nagl *et al.* 1998) four such species had been identified—without which precision comparisons are of scant value. In fact, as their map and table 1 show, apart from localities near lakes, rivers in the Lake Victoria drainage were scarcely explored.

Among the riverine species named in their earlier paper is *Astatotilapia bloyeti*, formerly *Haplochromis bloyeti*, which some may still prefer to regard it as. This species or species complex is widely distributed throughout the Lake Victoria drainage and far beyond it, both to the south and east and west to the Niger drainage (Greenwood 1979), though some records are questionable. Among the putative ancestors of the Lake Victoria flock it has claims that merit serious consideration. Although interesting, the frequencies of certain alleles revealed by the earlier investigation of Nagl *et al.* (1998) in named lacustrine endemic and riverine haplochromines, including *A. bloyeti*, provide little information on this matter.

We are not concerned here with phylogenetic details, nor with the fact that the limitations of the material indicate a greater age (160 000 years) for subgroup VC than for what is believed to be the older VD (110 000 years). What is relevant is that Nagl *et al.* (2000) nevertheless say that 'it is highly improbable' that divergence of subgroup VC took place 12 000 years ago or less. They then make the apparently contradictory statement that the latter conclusion 'does not preclude the possibility that the morphological divergence of the species comprising subgroup VC occurred during the 12 000 year interval' (p.1057) and indeed they argue that it probably did. Their explanation seeks to reconcile these apparently contradictory statements.

## 5. A REJECTED EXPLANATION

In an earlier study Nagl *et al.* (1998) showed that what they assumed to be neutral polymorphisms are shared by several Lake Victoria haplochromines and their riverine relatives. Different polymorphisms were found in cichlids from Lakes Tanganyika and Malawi so, to simplify a more complex situation, the Lake Victoria polymorphisms must have arisen after the ancestors of these flocks diverged but before those of the Lake Victoria flock

colonized the lake. Earlier studies (Sage *et al.* 1984) had indicated that the Lake Victoria haplochromines were invariant at the molecular level.

Using this information, Nagl *et al.* (2000) suggest that the mutations responsible for the morphological adaptations of the lacustrine endemics of Lake Victoria 'must have already been present in the founding population as polymorphisms, but in combinations which allowed the maintenance of the generalist phenotype characteristic of riverine haplochromines' (p.1060). Only after the lake was supposedly recolonized, when they became subjected to selection pressures to produce a range of adaptive lacustrine phenotypes, were the mutations allegedly 'sorted out into new combinations' which gave rise to the required specialized phenotypes. They also assume that the founding population of the flock must have been large in order to furnish the necessary polymorphisms. Because they believe that the radiation time was very short (which is not only far from proven but seems highly improbable) they believe that species of the Lake Victoria flock cannot be expected to be fixed for any mutations other than those responsible for the morphological differences between them.

This idea is not entirely new. It has echoes of that of Kaufman *et al.* (1997) who suggested that the Lake Victoria haplochromine flock shares a common genome that may be capable of producing a range of adaptive types with little readjustment. As they put it, any individual species may contain most of the information required to produce all the others.

While intriguing, Nagl *et al.*'s (2000) suggestion seems to be an improbable hypothesis tailored to fit an event that may never have happened. First, polymorphisms shared by endemic haplochromines and riverine species are of no significance in the present context unless the riverine species concerned were proven ancestors of the Lake Victoria flock. It is also not known with what attributes the polymorphisms revealed are concerned and no polymorphisms related to any morphological feature have been demonstrated. Furthermore, whatever the mechanism involved, it still suggests that the Lake Victoria haplochromine flock arose from 'a non-specialised riverine founding population that colonised the forming L.V[ictoria] some 12 400 years ago' (Nagl *et al.* 2000, p.1060), that the flock 'must have therefore arisen within this short period of time' (p.1060) and that the morphological specializations did likewise. To understate the matter, it is very difficult to believe that all (or most) of the mutations responsible for the enormous array of morphological and other specializations of the species flock were 'stored' in riverine forms adapted to this way of life, and only expressed themselves in the appropriate way when lacustrine conditions returned. Even if riverine species conserved some such potentialities, it seems inconceivable that even a handful of such forms (rivers generally support only small numbers of cichlid species) could carry the potential to produce probably more than 600 species, some of them very specialized, in some 12 000 years. Moreover, the finding of a few polymorphisms of unknown expression does not justify extrapolation to infer that unexpressed genes controlling the development of morphological structures of great complexity, and of many kinds, were ever carried by the ancestors of the

haplochromine flock. If the founding population(s) needed to be large, this adds the further difficulty of explaining where such a large population took refuge during the drought.

Such inherent problems apart, the major weakness of the hypothesis is that, like all other suggested histories that accept a Late Pleistocene desiccation of Lake Victoria, it completely overlooks the fact that such an event would eliminate not only the haplochromines, but also the entire biota of the lake. This means that all its other endemic organisms must have achieved this status within *ca.* 12 000 years. Credulity is strained beyond its limits to believe that all the other endemics of Lake Victoria displayed the same (unproven and improbable) phenomenon as that suggested by Nagl *et al.* (2000) for the haplochromines; that, whatever the explanation, all could evolve with amazing rapidity; or that all of them could survive for millennia adjacent to Lake Victoria in rivers, the very existence of which at the relevant time would be remote. If the lake dried out and refilled as recently as claimed, all these phenomena demand explanation and proof. Until this is provided, neither the drying out of the lake nor the rapid evolution of the haplochromine flock that allegedly followed its refilling can be treated seriously.

## 6. A COMMENT ON SOME RECENT SUGGESTIONS

Since this paper was submitted, the alleged Late Pleistocene desiccation of Lake Victoria has been mentioned by several authors in a volume on ancient lakes (Rossiter & Kawanabe 2000). Most refer to it only in passing but Seehausen (2000, p. 241) says that 'it is beyond doubt that, if not entirely dried up, only a shallow, although extensive, swamp could have persisted, possibly with seasonal pools'. It is far from beyond doubt that the lake 'entirely dried up' and Seehausen (2000) himself offers a very different alternative. Nor can the doubt be removed unless Kendall's (1969) detailed radiocarbon-dated study of a sediment core is shown to be incorrect. This showed that sediments were accumulating even in shallow inshore regions at a time when the lake was allegedly dry. More importantly, however convincing the geophysical data appear to be, their validity is suspect if they are not in accord with the current biological situation and incompatible with any plausible recent history of the aquatic fauna of the region.

If, on the other hand, as Seehausen (2000) suggests, a shallow swamp persisted, this not only repudiates the claim that Lake Victoria dried out completely but destroys the argument for express speciation and rapid morphological differentiation of the haplochromine cichlids. The biological evidence strongly suggests that a diverse aquatic fauna survived in the Lake Victoria basin throughout the period in question, and even reduction of the lake to an extensive swamp would permit this. A plausible model for such a swamp exists. Lake Bangweulu (area *ca.* 2072 km<sup>2</sup>), of which lake and its contiguous swamps I have personal experience, has a maximum depth of 10 m and most of it is much shallower. Its enormous swamps, which were beautifully mapped by Debenham (1952), indicate what such a swamp would be like. The area of permanent swamp includes dozens of

lakelets (some of them bigger than Windermere, England's largest lake) that support a rich and diverse fauna of fishes and invertebrates. Contrary to what Seehausen (2000) suggests (the marginal swamps of Lake Victoria are less informative in this respect) such lakelets could serve as refuges, and would be conducive to allopatric speciation, as could any lakes like the present-day Lake Nabugabo (area 28.5 km<sup>2</sup> and maximum depth 4.6 m), which is cut off from Lake Victoria, which hosts both cichlid and non-cichlid fishes. The endemic non-cichlid fishes of Lake Victoria, in particular *X. eupogon* and the open-water shoaling *Rastrineobola argenteus*, which has its own endemic parasitic copepod *Lernaea inflata*, and such a cichlid as the tilapiine *O. esculentus*, suggest that considerable areas of open water, some of it possibly deep, persisted in the basin. When the lake became deeper, any such lakelets would inevitably fill with sediment before more elevated areas that supported emergent or marsh vegetation did so. After several millennia this would give rise to the relatively even-surfaced lake bed revealed by seismic reflections. If fishes, of all families, did not survive in the Lake Victoria basin, where did they or their immediate ancestors find refuge during a dry period?

The question of refuges, always difficult to explain, is now even more so in the light of the molecular evidence adduced from the haplochromine cichlids by Nagl *et al.* (2000). In fact, in his otherwise excellent paper, Seehausen (2000) addressed none of the questions that have to be answered before it can be claimed that the cichlid flock of Lake Victoria originated only *ca.* 12 000 years ago. In particular he ignores the crucial fact that, if this was the case, all the other endemics of the lake must have done likewise. It is difficult to explain such rapid evolution in the haplochromine cichlids, as Nagl *et al.* (2000) make plain. It is much more difficult to explain why, of all the world's lakes, it was uniquely in Lake Victoria that a rich assemblage of fishes of several families and many invertebrates of diverse affinities evolved in such a short period of time. If such rapid speciation in many groups is possible, and happened many times in one lake, one would expect to find endemic species in many lakes older than *ca.* 12 000 years, but this is not the case.

It is particularly pertinent to observe that the non-cichlid endemics of Lake Victoria conspicuously lack the means of employing such attributes as disruptive sexual selection based on coloration that have been suggested as having contributed to the rapid speciation of cichlids (e.g. Seehausen 2000).

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